RESEARCH PAPER

ENVIRONMENTAL CONTROLS OF PHOTOSYNTHETIC PARAMETERS IN FOUR DOMINANT BOREAL TREE SPECIES: CONTRASTING RESPONSES OF DECIDUOUS ANGIOSPERMS AND EVERGREEN GYMNOSPERMS

Vladislava B. Pridacha[1,*], Alexander V. Olchev[2]

[1]Forest Research Institute, Karelian Research Centre, Russian Academy of Sciences, Pushkinskaya St.,11, Petrozavodsk, 185910, Russia

[2]Faculty of Geography, Lomonosov Moscow State University, GSP-1, Leninskie Gory, Moscow, 119991, Russia

***Corresponding author:** pridacha@krc.karelia.ru

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ABSTRACT. Boreal forests play a crucial role in maintaining the global ecological balance, acting as significant carbon sinks and mitigating the effects of climate change. This study examined how temperature affects photosynthesis in four boreal tree species – *Pinus sylvestris, Betula pendula, Populus tremula,* and *Alnus incana* – growing in a clear-cut of mid-taiga bilberry-type pine forest in southern Karelia, Russia. The Farquhar biochemical model was used to analyze key photosynthesis parameters, such as the maximum carboxylation rate by Rubisco (Vc_{max}), the maximum photosynthetic electron transport rate (J_{max}), and the triose phosphate utilization (*TPU*) rate, under different leaf temperatures ranging from 20 to 35°C and light conditions. The results revealed significant interspecific differences in photosynthetic responses. At a leaf surface temperature of 25°C, the lowest Vc_{max25}, J_{max25}, and TPU_{25} values were obtained for the 1-year-old needles of *P. sylvestris* (38.8, 70.7, and 5.5 µmol m^{-2} s^{-1}), whereas the values were 1.5- to 2.4-fold higher for the leaves of *B. pendula* (93.5, 172.1, and 12.7 µmol m^{-2} s^{-1}), *A. incana* (86.1, 155.1, and 11.4 µmol m^{-2} s^{-1}), and *P. tremula* (58.6, 122, and 9.3 µmol m^{-2} s^{-1}). Meanwhile, *P. sylvestris* and *B. pendula* had a broader optimal temperature range for Vc_{max} and J_{max} (20–35°C), whereas *A. incana* and *P. tremula* had a narrower range (20–30°C), experiencing a decline at 35°C. In addition to having different levels of resistance to extreme temperatures, deciduous species also differed in their responsiveness to CO_2 enrichment. This could lead to shifts in the composition of boreal forest species under changing climate conditions. *P. sylvestris* demonstrated greater stability at low light levels and a strong response to elevated CO_2, indicating its high adaptability to future climate change. These results highlight the importance of considering species characteristics when predicting the carbon balance of boreal forests. They can be used to model the resilience of forest ecosystems under climate change and to plan further investigations, including studies of mature trees and the effects of additional stress factors, such as drought.

KEYWORDS: boreal forests; photosynthetic CO_2 response curve; photosynthetic light response curve; temperature dependence; climate change

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INTRODUCTION

Boreal forests play a crucial role in maintaining the Earth's ecological balance. As long-term carbon sinks, they mitigate the effects of climate change by reducing the concentration of greenhouse gases in the atmosphere. They also regulate the balance of water and heat, directly influencing regional and global climates (Bonan, 2008; IPCC, 2023; Gushchina et al., 2023; Olchev, 2025). Meanwhile, the current climate, characterized by rising global temperatures, changing precipitation patterns and higher frequency of regional hydrological and meteorological anomalies (Mokhov, 2022), increases the risk of irreversible alteration in the structure and functions of forest ecosystems (Olchev et al., 2013; Groisman et al., 2017). Changes in the growth, productivity, and mortality of boreal tree species can affect taiga forests' ability to absorb carbon dioxide (CO_2) from the atmosphere. It is crucial to understand and predict the consequences of climate change for deciduous and coniferous tree species because their capacity to absorb CO_2 through photosynthesis directly impacts the global carbon cycle and the overall state of forest ecosystems (Tselniker et al., 1993; Molchanov, 2007; Suvorova & Popova, 2015; Olchev & Gulev, 2024).

Photosynthesis is the physiological basis of plant productivity. There are many mathematical models that describe photosynthesis at various scales, ranging from molecular interactions in thylakoid membranes to a whole plant or ecosystem (Laisk et al., 2009; Hikosaka et al., 2016; Sukhova et al., 2021). The Farquhar approach (Farquhar et al., 1980; von Caemmerer et al., 2000) is traditionally used to model net photosynthesis in tree leaves and ground vegetation. It has proven effective in predicting CO_2 assimilation under various environmental conditions (Bernacchi et al., 2013; Busch et al., 2024; Stirbet et al., 2024). The model enables determining several key parameters, including the maximum carboxylation rate (Vc_{max}), maximum rate of electron transport for the acceptor molecule ribulose 1,5-bisphosphate regeneration under saturating light (J_{max}), triose phosphate utilization (*TPU*) rate, as well as dark respiration (R_d) rate and mesophyll conductance (g_m).

The parameters Vc_{max}, J_{max}, and *TPU* are essential for modeling photosynthetic responses to environmental changes. Vc_{max} and J_{max} depend strongly on external conditions, particularly CO_2 concentration and light intensity (Busch et al., 2024). Solar radiation directly impacts photosynthesis because it provides to energy for electron transport and CO_2 reduction. Light activation occurs through covalent and conformational modifications of enzymes that catalyze Calvin cycle reactions, particularly ribulose bisphosphate carboxylase/oxygenase (Rubisco) (Laisk et al., 2009). Light also influences CO_2 diffusion between the air and the intercellular space of the leaf by regulating the width of the stomatal openings. An increase in air CO_2 content contributes to enhanced Rubisco carboxylation activity (Norby et al., 2005). Electron transport is also sensitive to environmental factors as it depends on the stability of the thylakoid membrane (Hikosaka et al., 2016) and can vary widely even within a species (Bernacchi et al., 2013). The third parameter that limits photosynthesis is *TPU*, which is related to the export and utilization of triose phosphates. *TPU* reflects the capacity to synthesize starch in chloroplasts or export metabolites to the cytosol for sucrose synthesis (Sharkey, 2024). Sucrose is then transported through the phloem to the plant's heterotrophic tissues and organs. High rates of sucrose phosphate synthesis can deplete the pool of free inorganic phosphate, thereby limiting photophosphorylation (Sharkey, 1985; von Caemmerer, 2000). *TPU* primarily restricts photosynthetic carbon fixation under high CO_2, high light intensity, or low temperature (Bernacchi et al., 2013; Busch et al., 2024). The importance of assessing the temperature dependence of photosynthesis parameters is emphasized in the works of Medlyn et al. (2002), Lin et al. (2013), and Togashi et al. (2018). These parameters are crucial for predicting how vegetative cover will respond to the expected increase in air temperature and CO_2 concentrations in the future.

Some studies have shown that photosynthetic parameters can vary depending on a plant's species or functional type (Medlyn et al., 2002; Lin et al., 2013). According to Wullschleger (1993) and Mandela et al. (2022), higher Vc_{max}, J_{max}, and *TPU* values have been observed in annual herbaceous plants (75, 154, and 20 μmol m^{-2} s^{-1}) than in perennial woody species (44, 97, and 5 μmol m^{-2} s^{-1}). Interspecific differences in photosynthetic parameters have also been noted in forest tree species (Medlyn et al., 2002; Korzukhin & Tselniker, 2009; Pridacha et al., 2022) and are associated with leaf mesostructure, growth, and development in different species during the growing season (Tselniker et al., 1993; Oleksyn et al., 2000; Juárez-López et al., 2008).

The most common tree species in boreal forests belong to the genera *Pinus, Betula, Populus*, and *Alnus* (Afonin et al., 2008). Despite occupying similar areas and having a wide ecological amplitude, boreal tree species, particularly *Pinus sylvestris* L., *Betula pendula* Roth, *Populus tremula* L., and *Alnus incana* (L.) Moench, exhibit noticeable ecophysiological differences. In a previous study, we examined how microclimatic and edaphic conditions of clear-cutting influence the functional characteristics of evergreen gymnosperm and deciduous angiosperm tree species. We identified species-specific changes in the photosynthetic water and nitrogen use efficiency and nutrient ratios in Scots pine, silver birch, aspen, and grey alder along the "clear-cut site – bilberry-type pine forest" gradient of environmental factors (Pridacha et al., 2021).The interspecific features of the consistency of xylem hydraulic characteristics and CO_2/H_2O gas exchange parameters in the leaves of the different species indicates that Scots pine and aspen have a more efficient and safer hydraulic structure as compared with silver birch (Pridacha et al., 2023). However, during a three-year observation period in the warm season, lower photosynthesis and dark respiration rates were obtained in Scots pine than in deciduous tree species (Pridacha & Semin, 2024).

Due to the low boreal tree species diversity, changes in CO_2 gas exchange parameters of each species resulting from environmental disturbances and climate change can significantly affect the carbon budget of taiga forests (Kurepin et al., 2018; Dusenge et al., 2020; Gagné et al., 2020). However, despite the recognized importance of assessing photosynthesis parameters for modeling and predicting carbon fluxes in terrestrial ecosystems (Laisk et al., 2009; Hikosaka et al., 2016), the impact of environmental changes on these parameters is still not fully understood. To address the lack of knowledge in this area, we examined the effects of temperature on photosynthesis parameters in co-growing an evergreen gymnosperm (*Pinus sylvestris* L.) and three deciduous angiosperm (*Betula pendula* Roth, *Populus tremula* L., and *Alnus incana* (L.) Moench) tree species in a clear-cut of mid-taiga bilberry-type pine forest. The choice of experimental design was based on the fact that clear-cuts are an ideal subject for studying how plant communities respond to environmental changes because the processes occurring in them are primarily influenced by natural factors. The working hypothesis of the study was that different tree species that grow together would show similar responses to environmental changes in the European North. Analyzing the relationship between photosynthesis parameters and environmental factors helps us understand the mechanisms of plant adaptation in response to environmental changes, particularly in the context of climate change.

MATERIALS AND METHODS

Study area and tree-growing conditions

The study was carried out in July 2018 in the European part of the middle taiga forest zone (Republic of Karelia) on a 10-year-old, clear-cut of bilberry-type pine forest (62°10′28.1′′N, 33°59′58.8′′E). According to the Köppen climate classification system, the climate of the study area is humid continental with cool summers (Peel et al., 2007). The area is characterized by high relative humidity (averaging 75%) and significant precipitation throughout the year (550–750 mm), 350–400 mm of which falls during the snow-free period from May to October (Nazarova, 2021). According to the climatic means for the period from 1991 to 2020, the average annual air temperature is +3.6°C, with minimum and maximum values of –8.4°C and +17.1°C in January and July, respectively. The average air temperature during the growing season (May–September) is +13°C. The total radiation balance for the growing season is 1,130 MJ m^{-2}. According

to data from the Kondopoga weather station, the growing season from May to September of 2018 in the study area was relatively warm (0.7°C <ΔT_{seas}: < 3.0°C) and characterized by a precipitation deficiency relative to the long-term climatic mean in May, June, and July (44, 52, and 77% of the climatic means, respectively), followed by a rainy August (151% of the climatic mean).

The study examined 10-year-old Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), aspen (*Populus tremula* L.), and grey alder (*Alnus incana* (L.) Moench) trees growing in a clear-cut bilberry-type pine forest site. The young stand that formed through natural regeneration in the clear-cut are primarily Scots pine (70%), with a mix of silver birch and aspen trees. The understory consists of grey alder, willow, and rowan (Pridacha & Semin, 2024). Five model trees have been selected for each of the species in the clear-cut site. The highest recorded values for height and trunk diameter at the site were for grey alder (4.5 ± 1.3 m and 4.3 ± 1.7 cm, respectively) and silver birch (3.4 ± 0.2 m and 1.8 ± 0.2 cm, respectively). The lowest values were observed for Scots pine (2.3 ± 0.1 m and 1.6 ± 0.1 cm, respectively) and aspen (1.8 ± 0.5 m and 1.2 ± 0.4 cm, respectively) (Pridacha et al., 2021).

The soil in the site was an Arenic Albic Podzol. Roots were mostly concentrated within 2–25 cm depth. The ground water table depth was 1.2 m. The detailed characteristics of the vegetation and soil cover of the clear-cut site have been presented in previous studies (Pridacha et al., 2021; Pridacha & Semin, 2024).

Parameters of CO_2 gas exchange

Field measurements of key photosynthetic parameters were conducted in July 2018 in the clear-cut bilberry pine forest site on the leaves of *B. pendula, P. tremula, A. incana* and on the 1-year-old needles of *P. sylvestris*. Measurements were taken during daylight hours from 10 a.m. to 4 p.m. on intact leaves in the middle part of the plant's crown. A portable photosynthetic system LI-6400XT (LI-COR Inc., USA) was used for the measurements. The system was equipped with a CO_2 injector, a standard 2 cm × 3 cm leaf chamber, and a LI-6400-02B LED light source (LI-COR Inc., USA). Healthy, fully formed leaves without visible damage were sampled from all plants using a uniform method with three biological replicates for each species. All the experiments were conducted under similar weather conditions.

The photosynthesis measurement program involved obtaining light and carbon dioxide response curves for photosynthesis parameters at leaf (needle) surface temperatures ranging from 20°C to 35°C. Both response curves were measured separately at each leaf temperature (20, 25, 30, and 35°C). The range of leaf temperatures was chosen based on the plant growth temperature (20°C), a reference temperature (usually 25°C), and temperatures above 20°C (30–35°C). The average leaf adaptation time to chamber conditions was about 15 minutes. The CO_2 response function of CO_2 gas exchange in leaves (A/Ci-curve) was determined by sequentially changing the CO_2 concentration in the leaf chamber (400, 300, 200, 100, 60, 30, 400, 600, 800, 1000, 1200, and 1600 µmol CO_2 mol^{-1}) at a saturating light intensity of 1600 µmol m^{-2} s^{-1}, in accordance with the device's standard configuration (Busch, 2024). *A/Ci*-curve measurements were also performed under lower light conditions (400 and 100 µmol m^{-2} s^{-1}) in a leaf chamber at a leaf surface temperature of 25°C. The relative humidity in the measuring chamber was set to 50% to prevent stomatal closure during the measurements.

The light response of photosynthetic parameters (*A/Q*-curve) was determined by measuring the intensity of CO_2 gas exchange at various PAR values (1600, 1200, 900, 600, 300, 150, 100, 75, 50, 25, and 0 µmol m^{-2} s^{-1}) under constant CO_2 concentrations (400 µmol CO_2 mol^{-1}) and relative air humidity (50%) in the leaf chamber. The *A/Q*-curve measurements were also performed at higher CO_2 concentrations (800 and 1200 µmol CO_2 mol^{-1}) and a leaf temperature of 25°C.

The CO_2 response curves (*A/Ci*-curve) were used to calibrate the key parameters of the Farquhar photosynthesis model (Farquhar et al., 1980) as modified by Sharkey et al. (2007): maximum carboxylation rate (Vc_{max}), electron transport rate at light saturation (J_{max}), triose phosphate utilization rate (*TPU*), and dark respiration rate (R_d). The temperature dependencies of Vc_{max}, J_{max}, and *TPU* were obtained by statistically evaluating a set of the photosynthesis parameter values at various leaf temperatures. Based on these dependencies, the standardized Vc_{max25}, J_{max25}, and TPU_{25} values were obtained at the selected reference temperature of 25°C (Sharkey et al., 2007; Sharkey, 2016).

The parameters of the light response curve model, particularly the value of photosynthesis at saturating PAR values (A_{max}), were calculated using a modified Michaelis–Menten function (Kaipiainen, 2009; Pridacha et al., 2022). Detailed procedures for assessing the carbon dioxide and light-response functions of CO_2 gas exchange have been reported in previously published studies (Sharkey et al., 2007; Sharkey, 2016; Busch, 2024).

The CO_2 gas exchange rates for *P. sylvestris* needles in our study were converted to the entire needle surface area. To calculate the surface area of the needles, we used a simplified method to determine their specific linear density (weight of unit needle length) (Tselniker, 1982).

Statistical analysis

Statistical data analysis was performed using Statistica 13.3 (TIBCO Software Inc., USA). Regression analysis was used to process the experimental data. Statistical significance was defined as $p < 0.05$. The diagrams show the means and their standard errors.

RESULTS

The classic biochemical Farquhar model and regression analysis of photosynthesis light response curves accurately describe how leaf photosynthesis responds to changes in ambient CO_2 concentrations and light conditions, with an R^2 value ranging from 0.95 to 0.99 (Fig. 1).

Analysis of the temperature dependence of photosynthetic parameters revealed that increasing leaf temperature within the 20–35°C range resulted in 5.6- and 3.1-fold increases in Vc_{max} in *P. sylvestris and B. pendula*, respectively (Fig. 2). In *A. incana* and *P. tremula*, Vc_{max} increased within a narrower temperature range (20–30°C) than in *P. sylvestris* and *B. pendula*. The increase was 2.2- and 3.1-fold, respectively, followed by a subsequent decrease of 1.2- and 2.1-fold at 35°C in *A. incana* and *P. tremula*, respectively. Analysis of the standardized Vc_{max25} values at a reference temperature of 25°C revealed similar patterns of change for this parameter in each species. The Vc_{max25} values were higher than the 20°C measured values (1.7-, 1.5-, 1.4-, and 1.5-fold for *P. sylvestris, B. pendula, A. incana*, and *P. tremula,* respectively) and lower at 30°C (1.4- to 1.6-fold) and 35°C (2- to 2.4-fold) for all species. At a leaf surface temperature of 25°C, Vc_{max} values were lowest for 1-year-old *P. sylvestris* needles (38.8 µmol m^{-2} s^{-1}) and highest for *B. pendula, A. incana*, and *P. tremula* leaves (93.5, 86.1, and 58.6 µmol m^{-2} s^{-1}, respectively).

The J_{max} values for *P. sylvestris* increased 2.5-fold within the temperature range of 20–35°C. However, the increase was

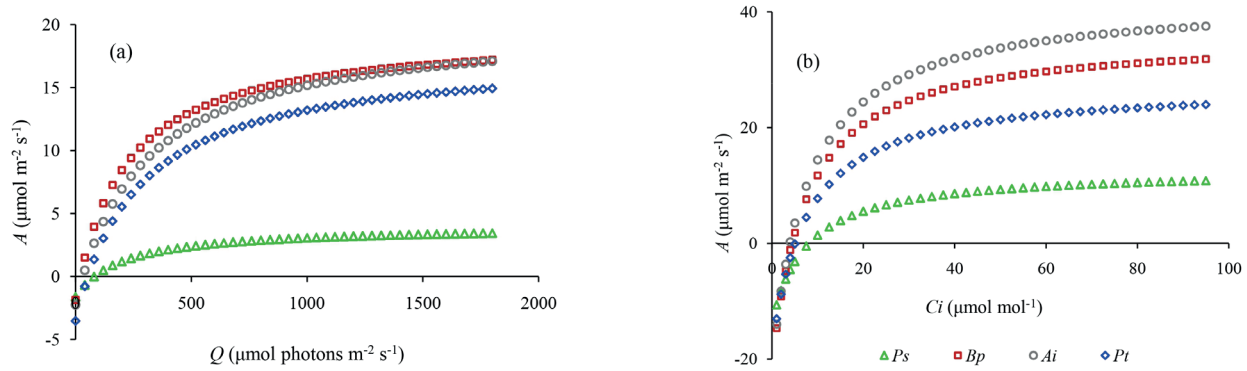

Fig. 1. Sample *A/Q*-curve (a) and *A/Ci*-curve (b) plotted for 1-year-old needles of *Pinus sylvestris (Ps)* and leaves of *Betula pendula (Bp), Alnus incana (Ai), Populus tremula (Pt)* at leaf temperature of 25°C using the LI-6400 XT protocol

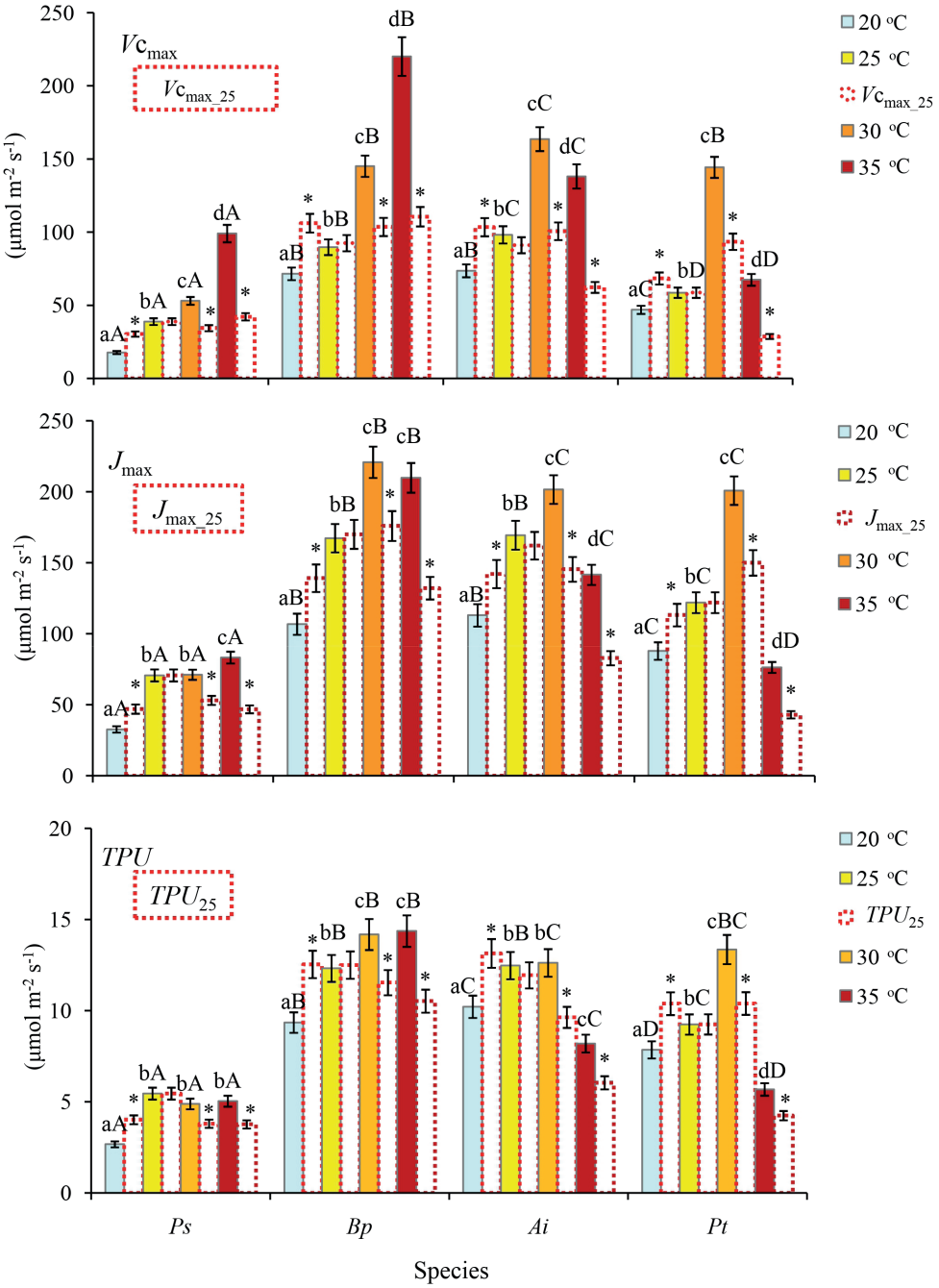

Fig. 2. Maximum rates of carboxylation by Rubisco (Vc_{max}), electron transport (J_{max}), and triose phosphate utilization (*TPU*) measured in the leaf temperature range of 20–35°C and standardized at a reference temperature of 25°C (Vc_{max25}, J_{max25}, and TPU_{25}) in *Pinus sylvestris (Ps), Betula pendula (Bp), Alnus incana (Ai),* and *Populus tremula (Pt)*. Different lowercase letters on top of the bars (a, b, c) indicate significant differences in means ($p < 0.05$) when comparing one species at different leaf temperatures, and different capital letters (A, B, C) indicate significant differences ($p < 0.05$) between different species at each treatment level. An asterisk (*) indicates a significant difference in means ($p < 0.05$) when comparing each pair of measured and standardized parameter values for each species

significantly lower, at only 1.2-fold, at temperatures between 25 and 35°C. For *B. pendula*, the J_{max} values increased 2-fold with an increase in leaf surface temperature from 20 to 35°C. For *A. incana* and *P. tremula*, this parameter increased up to 30°C (by 1.8 and 2.3 times, respectively) and then decreased at 35°C (by 1.4 and 2.6 times, respectively). Comparing the measured J_{max} values with the reference J_{max} values at 25°C revealed higher values for all species at 20°C (1.4, 1.3, 1.3, and 1.3 times higher for *P. sylvestris, B. pendula, A. incana,* and *P. tremula*, respectively). However, the corresponding values were lower at 30°C (by 1.3–1.4 times) and 35°C (by 1.6–1.8 times) in all species. The lowest J_{max25} values were observed for 1-year-old needles of *P. sylvestris* (70.7 μmol m^{-2} s^{-1}), compared to the deciduous species: 172.1, 155.1, and 122 μmol m^{-2} s^{-1} for *B. pendula, A. incana*, and *P. tremula*, respectively.

As the temperature of the leaf surface raised from 20 to 35°C, the *TPU* values increased 1.9-fold in *P. sylvestris* trees and 1.5-fold in *B. pendula* trees. For *A. incana* and *P. tremula*, the *TPU* values increased 1.2- and 1.7-fold, respectively, when the leaf temperature increased from 20 to 30°C. Then, it decreased 1.5- and 2.4-fold, respectively, at 35°C. As with Vc_{max} and J_{max}, higher referenced TPU values were observed for all species at 20°C than the measured values (1.5, 1.3, 1.3, and 1.3 times higher for *P. sylvestris, B. pendula, A. incana*, and *P. tremula*, respectively). Lower values were observed at 30°C (1.2–1.3 times lower) and 35°C (1.3–1.4 times lower) in all species. 1-year-old needles of *P. sylvestris* had the lowest TPU_{25} values (5.5 μmol m^{-2} s^{-1}) at a leaf temperature of 25°C compared to *B. pendula* (12.7 μmol m^{-2} s^{-1}), *A. incana* (11.4 μmol m^{-2} s^{-1}), and *P. tremula* (9.3 μmol m^{-2} s^{-1}) leaves.

Importantly, decreases in Vc_{max}, J_{max}, and *TPU* values occurred when the light intensity in the leaf chamber decreased from saturating to low levels at a leaf surface temperature of 25°C for all tree species (Fig. 3). At the same time, interspecific differences in the dynamics of these parameters were revealed. For example, *P. sylvestris* showed the smallest decrease in Vc_{max25}, J_{max25}, and TPU_{25} values (1.2-, 1.5-, and 1.5-fold, respectively) within the PAR range of 100 to 1,600 μmol m^{-2} s^{-1}compared to deciduous species (3.1- to 3.2-, 4.3- to 4.8-, and 4.1- to 4.4-fold, respectively). Conversely, a 4-fold decrease in light intensity (from 1,600 to 400 μmol m^{-2} s^{-1}) led to a smaller decrease in Vc_{max25}, J_{max25}, and TPU_{25} values in deciduous species (1.3–1.8, 1.4–1.6, and 1.4–1.6 times, respectively) than in *P. sylvestris* (J_{max25} and TPU_{25} by 1.3 times).

Analysis of A_{max} values revealed insignificant changes in *P. sylvestris, B. pendula*, and *A. incana* at leaf temperatures of 20–25°C, followed by a decrease in this parameter as the temperature increased to 35°C (decreasing by 1.9, 1.9, and 2.8 times, respectively) (Fig. 4a). *P. tremula* featured a greater stabilization of A_{max} in the 20–30°C range and a smaller decline in the parameter at 35°C (1.3 times) compared with other species. Increasing the CO_2 concentration in the leaf chamber to 800 and 1,200 μmol CO_2 mol^{-1} for all tree species

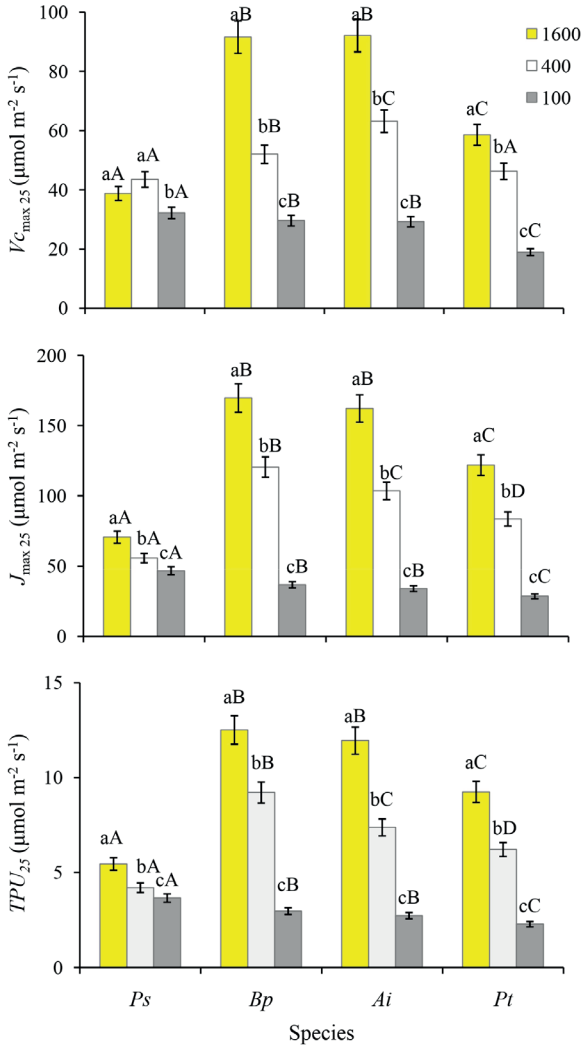

Fig. 3. Maximum rates of carboxylation by Rubisco (Vc_{max25}), electron transport (J_{max25}), and triose phosphate utilization (TPU_{25}) measured under different light intensities (100–1600 μmol m^{-2} s^{-1}) on 1-year-old needles of *Pinus sylvestris (Ps)* and leaves of *Betula pendula (Bp), Alnus incana (Ai),* and *Populus tremula (Pt)* at a leaf temperature of 25°C. Different lowercase letters on top of the bars (a, b, c) indicate significant differences in means (p <0.05) when comparing one species at different light intensity, and different capital letters (A, B, C) indicate significant differences (p <0.05) between different species at each light level.

resulted in higher A_{max} values at a leaf surface temperature of 25°C (Fig. 4b). *P. sylvestris* exhibited the greatest increase in the parameter, with a 2- and 3-fold increase in CO_2 concentration relative to external conditions (1.9 and 2.6 times, respectively) compared to deciduous species, such as *P. tremula* (1.4 and 1.6 times, respectively), *B. pendula* (1.1 and 1.9 times, respectively), and *A. incana* (1.7 and 2.1 times, respectively).

Analysis of the temperature dependence of the J_{max}/Vc_{max} ratio, calculated from measured values between 20 and 35°C, revealed a negative linear relationship for all tree species (Fig. 5a). The decrease of the parameter with an increase in leaf temperature from 25 to 35°C was 2.2, 2.0, 1.7, and 1.8 times for *P. sylvestris, B. pendula, A. incana*, and *P. tremula*, respectively. The J_{max25}/Vc_{max25} ratio, calculated using reference values at 25°C, exhibited similar dependence, taking the form of a "bell curve" with a pronounced peak at 25°C for all species studied (Fig. 5b). The increase in the J_{max25}/Vc_{max25} ratio in response to leaf temperature elevation in the 20–25°C range and its decline in the 25–35°C range were, respectively, 1.2 and 1.6-fold for *P. sylvestris* versus 1.3–1.4 and 1.4–1.5-fold for the deciduous species. It is also important to note the similarity of the J_{max25}/Vc_{max25} ratio at 25°C for *P. sylvestris, B. pendula,* and *A. incana* (1.8), as well as higher value for *P. tremula* (2.1).

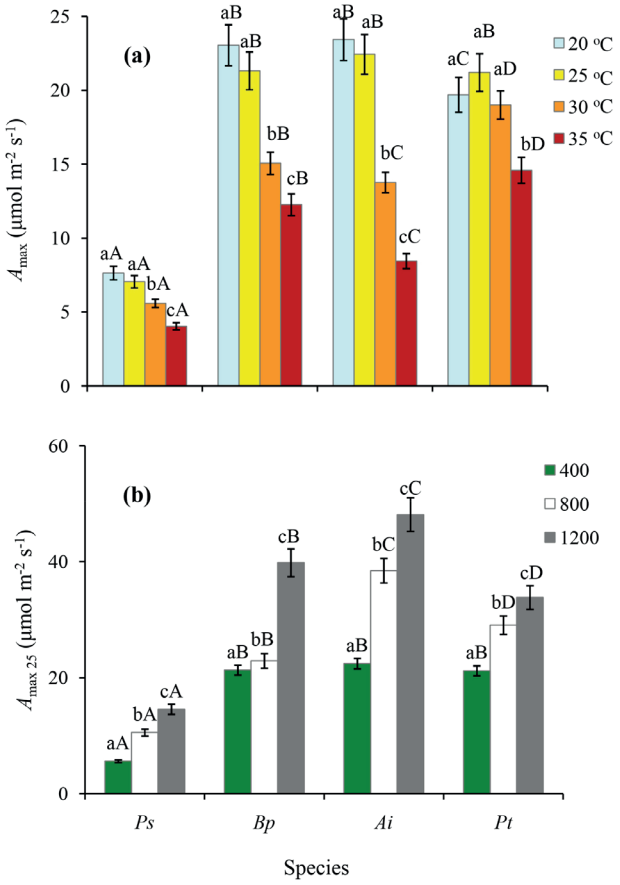

Fig. 4. Maximum CO_2 assimilation rate (A_{max}) measured at leaf temperatures ranging from 20 to 35°C (a) and at different CO_2 concentrations ranging from 400 to 1200 µmol CO_2 mol^{-1} at a leaf temperature of 25°C (b) on 1-year-old needles of *Pinus sylvestris (Ps) and leaves of Betula pendula (Bp), Alnus incana (Ai),* and *Populus tremula (Pt)*. Different lowercase letters on top of the bars (a, b, c) indicate significant differences in means (p <0.05) when comparing one species at different leaf temperatures or CO_2 concentrations, and different capital letters (A, B, C) indicate significant differences (p <0.05) between different species at each treatment level

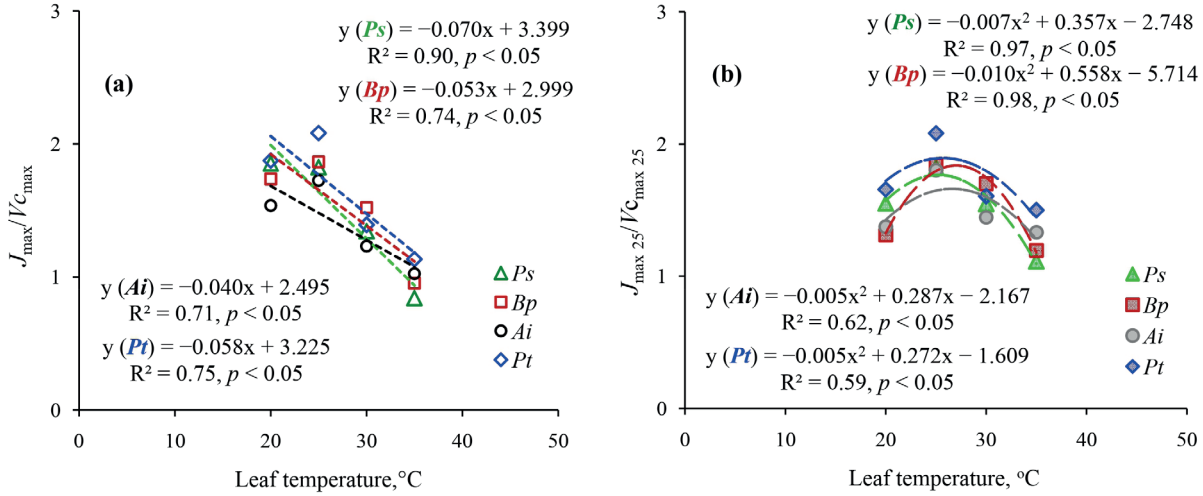

Fig. 5. Ratio of maximum electron transport rate (J_{max}) and maximum rate of carboxylation by Rubisco (Vc_{max}) measured at leaf temperature ranging from 20 to 35°C (a) and standardized at 25°C (b) in *Pinus sylvestris (Ps), Betula pendula (Bp), Alnus incana (Ai)* and *Populus tremula (Pt)*

DISCUSSION

Temperature dependence of photosynthesis parameters

The study examining the temperature dependence of photosynthetic parameters in four boreal tree species (*Pinus sylvestris, Betula pendula, Populus tremula*, and *Alnus incana*) revealed significant species-specific differences in the responses of Vc_{max}, J_{max}, and *TPU* to changes in leaf temperature and light conditions. These results provide a deeper understanding of how trees in cold climates adapt to changing environmental conditions, particularly in the context of global climate change.

Analysis of the temperature dependence of photosynthetic parameters (Fig. 2) revealed that *P. sylvestris* and *B. pendula* exhibited the greatest increase in Vc_{max} with temperature increases from 20 to 35°C. In contrast, *A. incana* and *P. tremula* demonstrated a narrower optimal temperature range (20 to 30°C) and a subsequent decrease in Vc_{max} at 35°C compared to 30°C. These results agreed with previous studies suggesting that coniferous species, including *P. sylvestris*, exhibit a broader temperature range for photosynthesis than deciduous species (Medlyn et al., 2002; Lin et al., 2013). The decrease in Vc_{max} in deciduous species at high temperatures may be related to the temperature-dependent activity of Rubisco, the inactivation of Rubisco due to reduced functioning of Rubisco activase, or the decreased stability of the enzyme (Sharkey, 1985; Galmés et al., 2015; Scafaro et al., 2023).

Similarly, J_{max} increased gradually in *P. sylvestris* and *B. pendula,* whereas *A. incana* and *P. tremula* exhibited a sharp increase in J_{max}, followed by a decrease, at 35°C. These results suggest that deciduous species, particularly *A. incana* and *P. tremula*, have more sensitive electron transport systems to elevated temperatures. This is likely due to the destabilization of thylakoid membranes and their components (Hikosaka et al., 2016). These results align with data indicating that high temperatures, which frequently occur during summer heat waves, can significantly limit the functioning of boreal deciduous species (Reich et al., 2018; Dusenge et al., 2020).

The *TPU* (triose phosphate utilization) parameter exhibited less variability in *P. sylvestris* and *B. pendula* than in *A. incana* and *P. tremula* within a temperature range of 25–35°C. This suggests that these species use carbohydrates (triose phosphates) more efficiently for synthesizing sucrose and starch under thermal stress compared to *A. incana* and *P. tremula*. However, the decrease in *TPU* in deciduous species at 35°C may result from limitations in starch and sucrose synthesis or phosphate recycling (Sharkey, 1985; von Caemmerer, 2000; Hikosaka et al., 2016). These findings have significant implications for long-term carbon accumulation under warming conditions.

The decrease in A_{max} observed in all species (Fig. 4a) as the temperature increases beyond the optimal range is due to the fact that the rate at which plants absorb CO_2 via photosynthesis is influenced by the photosynthetic apparatus and the degree of stomatal opening (Lin et al., 2012; Scafaro et al., 2023). Within the super-optimal temperature range, the decrease in photosynthetic intensity is due to a reduction in leaf turgor and stomatal closure. This hinders the diffusion of CO_2 from the atmosphere into the interior of the leaf and to the fixation centers. Additionally, as temperature rises, CO_2 solubility decreases, and the kinetic constants of carboxylating enzymes change (Sage & Kubien, 2007). As temperature increases, Rubisco's affinity for oxygen grows, enhancing photorespiration and reducing the efficiency of carbon dioxide fixation. This results in a decrease in the overall rate of photosynthesis.

It is important to note the greater thermal stability of A_{max} in *P. tremula* compared to other species across a broader temperature range (20–30°C), as well as the higher A_{max} values observed at sub-optimal temperatures (30–35°C). However, *P. tremula* exhibits lower photosynthetic activity than other deciduous species, as evidenced by lower Vc_{max}, J_{max}, and *TPU* values. Our observations align with prior research indicating that biochemical factors and mesophyll limitations primarily drive the decrease in photosynthesis in *P. tremula* at high temperatures and CO_2 concentrations (Hüve et al., 2019; de Souza et al., 2024). During four growing seasons at the same clear-cut site, we observed higher values of stomatal conductance and transpiration rate for *P. tremula* than for other deciduous species and *P. sylvestris* (Pridacha et al., 2021). These findings are important because stomatal conductance determines the rate of CO_2 diffusion to carboxylation sites (Baillie, Fleming, 2020; Márquez, Busch, 2024), and transpiration provides leaf thermoregulation by evaporating water from the leaf surface. This cooling effect prevents overheating, especially at high ambient temperatures (Lin et al., 2017; Drake et al., 2018). Thus, the greater thermal stability of A_{max} in *P. tremula* relative to other species can be due to higher CO_2 diffusion flux and better leaf thermoregulation. This is consistent with noted relative independence of CO_2 concentration in *P. tremula* leaf chloroplasts from temperature (de Souza et al., 2024).

Additionally, the greater thermal stability range of A_{max} in *P. tremula* may be due to differences in hydraulic regulation among species, specifically the anisohydric nature of *P. tremula* compared to the isohydric characteristics of *B. pendula* (Pridacha et al., 2023). This hypothesis is supported by data from other studies (Klein, 2014; Meinzer et al., 2016; Sellin et al., 2019, 2022). A previous study (Mäenpää et al., 2011) on the effects of ozone and temperature on carbon assimilation in *B. pendula* and *P. tremula* seedlings found that *B. pendula* leaves experienced a greater decrease in stomatal conductance (1.7 times) than *P. tremula* leaves (1.2 times) when the air temperature increased by 1°C. This is consistent with the more pronounced decrease in A_{max} in *B. pendula* with an increase in temperature above the optimum relative to *P. tremula* (Fig. 4a). This is likely because of a greater decrease in CO_2 diffusion flux into the leaf due to stomatal limitation of photosynthesis, despite higher activity of the photosynthetic apparatus in *B. pendula* (Fig. 2).

At the same time, in all species we observed a similar consistent pattern of the J_{max}/Vc_{max} ratio at temperatures between 20 and 25°C, which decreased as the temperature increased up to 35°C (Fig. 5). Despite interspecific differences, this pattern can be explained by the optimal temperature range for photosynthesis in C_3 plants, which is typically between 20–25 °C for most C_3 plants in the temperate zone (Laisk et al., 2009; Hikosaka et al., 2016). The decrease in the J_{max}/Vc_{max} ratio from 1.7–2.1 to 0.8–1.1 with increasing temperature for all species may be associated with the higher activation energy for Vc_{max} relative to J_{max}. Similar observations have been made by scientists studying other woody plants (Onoda et al., 2005; Ow et al., 2008; Riikonen et al., 2009). The similarity of the Rubisco specificity factor in gymnosperms and C_3 angiosperms has also been noted, as a measure of the enzyme's capacity to exhibit carboxylase and oxygenase activity relative to RuBP. This similarity is explained by the adaptation of Rubisco in different phylogenetic groups of plants to current CO_2/O_2 atmospheric levels (Miyazawa et al., 2020).

Response to light and CO_2

The study also revealed interspecific differences in photosynthetic responses to changes in light intensity and CO_2 levels. *P. sylvestris* exhibited greater stability in Vc_{max} and

J_{max} at low light levels (100–400 μmol m^{-2} s^{-1}). In contrast, deciduous species demonstrated a more significant decline in these parameters (Fig. 3). This may reflect conifers' adaptation to shading or high cloud cover in boreal regions (Oleksyn et al., 1998; Ma et al., 2014; Schmiege et al., 2023). Due to their higher photosynthetic activity, deciduous trees likely experience more pronounced inhibition of Rubisco activity at low light levels due to the strong binding of RuBP and other sugar phosphates formed during the Calvin cycle to the catalytic center (Sharkey, 1985; von Caemmerer, 2000).

At elevated CO_2 concentrations (800–1200 μmol mol^{-1}), the greatest increase in A_{max} was observed in *P. sylvestris* (Fig. 4b), suggesting a stronger response to CO_2 enrichment than in deciduous species. These results are consistent with previous studies (Niinemets et al., 2011; Kurepin et al., 2018) that reported conifers' superior adaptation to elevated CO_2 levels. Since CO_2 is a substrate for photosynthesis, its availability and concentration determine the activity of carbon metabolism. The increase in photosynthesis rate with increasing CO_2 levels is due to the realization of the carboxylase potential of Rubisco and the formation of a large RuBP acceptor pool in chloroplasts under these conditions (von Caemmerer, 2000; Busch et al., 2024). Among the deciduous species, the greatest increase in A_{max} with CO_2 growth was found in *A. incana*. We previously observed the highest values of specific nitrogen content and its biological absorption coefficient in *A. incana* relative to other species using the same model trees in the clear-cut (Pridacha et al., 2021). These results are consistent with previous studies reporting that trees of the genus *Alnus* can maintain high levels of photosynthesis after prolonged exposure to elevated CO_2 in nitrogen-poor soils due to high nitrogen availability from symbiosis with nitrogen-fixing actinomycetes (Vogel, Curtis, 1995; Rytter, Rytter, 2016). However, the weak response of *P. tremula* to increased CO_2 may indicate Rubisco activity saturation due to a greater supply of substrate (CO_2) in the leaf caused by the higher stomatal conductance of *P. tremula* leaves (Pridacha et al., 2021) or limitations in subsequent metabolic processes (Busch et al., 2024).

It is important to note that the influence of mesophyll conductance on photosynthesis has been demonstrated for all plant functional types (Flexas et al., 2014; Nadal et al., 2021; Knauer et al., 2022). In our study, coniferous species exhibited the lowest photosynthesis parameter values under all temperature, light, and CO_2 treatments compared to deciduous species. This finding aligns with prior studies indicating lower mesophyll conductance in coniferous trees than in deciduous trees, primarily due to the structural organization of their rigid leaves. Specifically, needles have thick mesophyll cell walls and chloroplasts, as well as a low ratio of chloroplast surface area to intercellular space per unit of leaf surface area (Veromann-Jürgenson et al., 2017; Carriquí et al., 2020). The low photosynthesis rates in coniferous trees are believed to be offset by their significantly longer active photosynthesis duration compared to deciduous trees in the boreal zone (Vasfilov, 2016; Shiklomanov et al., 2020). As temperatures and CO_2 levels in the atmosphere rise in a changing climate, it is assumed that species with low mesophyll conductance, particularly evergreen gymnosperm, will gain an advantage over deciduous angiosperm tree species in terms of distribution, especially in the boreal zone (Niinemets et al., 2011; Flexas et al., 2014; Nadal et al., 2021).

The results of our study are consistent with previously published data, while also revealing some new findings. For example, Medlyn et al. (2002) observed similar Vc_{max} values for *P. sylvestris* at 25°C. However, our data show that this parameter is more sensitive to extreme temperatures. The decrease in J_{max} in deciduous species at 35°C aligns with results obtained for temperate forest species (Togashi et al., 2018; de Souza et al., 2024), suggesting stability in photosynthetic temperature sensitivity across different plant biomes. Differences in *TPU* among species are consistent with Wullschleger's (1993) data, which showed lower *TPU* values in woody perennials than in herbaceous plants. Our study extends these findings by demonstrating how these differences manifest with changes in temperature and light intensity.

The results highlight the vulnerability of boreal deciduous species, especially *A. incana* and *P. tremula*, to climate warming due to decreased photosynthetic efficiency at high temperatures. At the same time, all species exhibit a similar consistent pattern of the J_{max}/Vc_{max} ratio within the 20–35°C temperature range. However, *P. sylvestris* demonstrates greater resilience, confirming its dominant role in boreal forests under future warming conditions (Bonan, 2008). Nevertheless, the stronger response of coniferous species to elevated CO_2 could be counterbalanced by other environmental stressors, such as drought. These factors were not considered in this study, yet they play a significant role in boreal ecosystem functioning (Reich et al., 2018; Liu et al., 2023; Martínez-García et al., 2024).

When considering the limitations of the identified patterns and prospects for future research, it should be noted that our study was conducted on young trees in a clear-cut area. This may not accurately reflect the functioning of a mature forest. Future studies should include mature trees and additional stress factors, such as drought and nutrient deficiency. Incorporating the data into ecosystem models based on the Farquhar approach will also improve predictions of the carbon cycle in boreal forests under climate change (Bernacchi et al., 2013).

CONCLUSIONS

Our study of the temperature dependence of photosynthetic parameters in four boreal tree species (*Pinus sylvestris, Betula pendula, Populus tremula*, and *Alnus incana*) revealed significant differences in their adaptation strategies to changing environmental conditions. *P. sylvestris* and *B. pendula* had a broader optimal temperature range for J_{max} and Vc_{max} (20–35°C), whereas *P. tremula* and *A. incana* had optimal values between 20 and 30°C and experienced a sharp decline at 35°C compared to 30°C. These results indicate their greater vulnerability to increased temperatures and global warming. Additionally, *P. sylvestris* showed greater resilience in photosynthetic parameters under low light conditions, as well as a more pronounced response to elevated CO_2 concentrations compared to deciduous species. This suggests its greater potential to adapt to future climate changes. The sensitivity of deciduous angiosperm tree species to extreme temperatures and increased CO_2 levels could lead to shifts in the composition of boreal forests in the future.

The results obtained are important for predicting the carbon balance of boreal ecosystems. The resilience of *P. sylvestris* to high temperatures and its efficiency in using CO_2 suggest that this species will maintain its dominant role in the warming climate. However, the vulnerability of deciduous angiosperm tree species requires further study, especially when considering additional stress factors such as drought. Integrating these data into the Farquhar approach-based ecosystem models will improve predictions of forest responses to climate change. Further studies should incorporate mature trees and complex stress scenarios to improve our understanding of the adaptive mechanisms of boreal species.

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